Euphytica (2018) 214:223
https://doi.org/10.1007/s10681-018-2283-3

Meta-QTL analysis and identification of candidate genes related to root traits in maize

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Received: 2 August 2018 / Accepted: 13 October 2018 / Published online: 13 November 2018

Abstract Maize root system architecture determines key functions of uptake of water and nutrients in plants. A large number of quantitative trait loci (QTLs) of root-related traits have been found in different populations of maize. Identification of consistent QTLs across diverse genetic backgrounds could be instrumental on marker-assisted selection of traits and identification of candidate functional genes. In this study, 20 published papers were investigated regarding on reported results of QTLs related to root traits of maize, and in total 428 individual QTLs for 23 root-related traits were used for meta-analysis, resulting in 53 Meta-QTLs (MQTLs) retrieved over ten maize chromosomes. Among these MQTLs regions, in total 45 maize homologs were considered as candidate genes affecting maize root traits by comparing with 7 genes from rice and 36 genes from *Arabidopsis*. Three maize genes (GRMZM5G813206, GRMZM2G167220 and GRMZM2G467069) identified from MQTL$_{8\text{-}5}$ could play important roles on lateral root and crown root development of maize. Two of the MQTLs, i.e. MQTL$_{7\text{-}2}$ and MQTL$_{9\text{-}1}$, involved in nitrogen (N) and phosphorus (P) stress responses and both of them with small physical distance (less than 3 Mb), could be used for abiotic stress improvement of maize root traits. These MQTLs and candidate genes will be helpful for future gene cloning and marker-assisted selection in maize.

Keywords Maize · Root trait · Meta-analysis · QTL · Candidate gene

Introduction

Root system is well known to have an essential role during plant growth, such as mechanical support, absorption and translocation of water and nutrients for the shoots (Lynch 2013; Villordon et al. 2014). Root system architecture displays a considerable degree of plasticity in response to the dynamic changing soil environments such as absorption of soil resources and resistance to stresses (Malamy 2005; Tai et al. 2016). For instance, the maize root depth and angle play important roles under resource-limiting conditions, such as drought, phosphorus and nitrogen deficiencies

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Electronic supplementary material The online version of this article (https://doi.org/10.1007/s10681-018-2283-3) contains supplementary material, which is available to authorized users.

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(Villordon et al. 2014; Hochholdinger 2016; Zhu et al. 2005).

Maize root system is composed of embryonic and post-embryonic roots (Freeling and Walbot 1994). The embryonic root system consists of a single primary root and a variable number of seminal roots (Hochholdinger et al. 2004). The primary root, the first organ that emerges after germination, in combination with the seminal roots are essential in the acquisition of water and nutrients at seedling stage (Lynch 2013). Therefore, embryonic root system reflects the typical early vigor of young maize seedlings (Peter et al. 2009). The post-embryonic root system initiating about few weeks after germination is composed of shoot-borne crown roots and brace roots (Hochholdinger and Tuberosa 2009). Lateral roots show conserved formation from all above-mentioned root types. The crown roots are the most important parts of the maize root system for acquiring soil resource during the vegetative growth stage. The 3D angle of the crown roots affects N and P capture from the soil layer (Zhu et al. 2005; Lynch and Brown 2001). The brace roots play an important role on the mechanical support of shoot, especially during the middle and late stage of the maize growth (Lynch 2013). Therefore, each component of root architectural traits has specific function during the consecutive stages of maize growth.

Root morphological traits of maize are distinctively controlled by multiple genes (Hochholdinger and Tuberosa 2009), however only a few of them have been cloned and characterized. *RTCS* (*rootless concerning crown and seminal roots*) is defective in the initiation of embryonic seminal roots and post-embryonic shoot-borne crown and brace roots (Taramino et al. 2007). *RUM1* (*rootless with undetectable meristem 1*), encoding a monocot-specific AUX/IAA protein, influences both embryonic seminal and post-embryonic lateral root initiation in primary root (von Behrens et al. 2011). Meanwhile, Salvi et al. (2016) found that two major SRN QTLs for the number of seminal roots co-mapped with the maize genes *rtcs* and *rum1*. *BIGE1* (*big embryo 1*) encoding a multidrug and toxin extrusion transporter affects the number of seminal and crown roots in maize (Suzuki et al. 2015). Additional four maize genes controlling root hair elongation have been cloned based on their mutant phenotypes. The root hair genes *RTH3* (Hochholdinger et al. 2008), *RTH5* (Nestler et al. 2014), and *RTH6* (Li et al. 2016a) are functionally associated with the cell wall-related processes such as cellulose organization, cell wall loosening and cellulose synthesis, respectively. In contrast, the root hair gene *RTH1* encodes the SEC3 subunit of the exocyst complex (Wen et al. 2005). And, *ZmPP2AA1* modulated phosphate-mediated root gravitropism by inhibiting primary root growth and stimulating the initiation of lateral roots (Wang et al. 2017). Taken together, these reported genes controlling the belowground root traits in maize are relatively few.

Quantitative trait Loci (QTL) mapping has become a powerful tool to identify genomic regions involved in the genetic variation of complex traits, including the root-related traits. In the past decades, a several QTLs have been reported in relation to various maize root traits based on different mapping populations (F_2, $F_{2:3}$, $F_{2:4}$, BC_1F_1, IL, BC_4F_3 and RIL etc.) under different growth conditions (Tuberosa et al. 2002; Hund et al. 2004; Zhu et al. 2005, 2006; Ju et al. 2006; Qiu et al. 2007; Liu et al. 2008; Chen et al. 2008; Trachsel et al. 2009; Cai et al. 2012; Osman et al. 2013; Burton et al. 2014; Li et al. 2015, 2016b; Hu et al. 2016; Salvi et al. 2016; Song et al. 2016; Liu et al. 2017; Zhang et al. 2018). However, the validity of QTL mapping results is influenced by many factors, including experimental conditions, type and size of mapping population, density of genetic markers, statistical methods and so on (Swamy et al. 2011). Thus, it is difficult to implement these reported QTLs directly to conduct molecular QTL cloning and MAS breeding practice. Vice versa, it is promising to integrate distinct genetic maps into a single consensus map and extracting information for the integral QTL fine-mapping and cloning (Veyrieras et al. 2007). Meta-analysis is an effective approach to combine the QTL results from independent studies and refining QTL position on the consensus map (Goffinet and Gerber 2000). Martinez et al. (2016) identified 84 MQTLs deriving from 808 unique QTLs related to yield in maize in 44 published studies, and found that QTL density was correlative with gene density. Actually, the first meta-analysis of four mapping populations for root traits had been performed in maize (Tuberosa et al. 2003). Moreover, 24 meta-QTLs (MQTLs) for the root length of maize have been determined by integration of nine populations from 15 QTL studies (Hund et al. 2011).

In this study, the published QTLs associated with 23 root-related traits in maize were collected, and meta-QTLs were retrieved through meta-analysis method based on the IBM2 2008 Neighbors reference map. The aims of the present Meta-QTL analysis were: (1) summarization of QTLs published between 2002 and 2018 regarding maize root-related traits, (2) refinement of QTL position related to root traits by meta-analysis, (3) identification of a set of promising candidate genes related to root traits.

Materials and methods

Preparation of QTL data

Twenty QTL studies related to maize root traits published from 2002 to 2018 were collected on the NCBI (https://www.ncbi.nlm.nih.gov/) (Table 1). A total of 517 independent QTLs were reported for 23 root-related traits in these studies (Table 2).

Consensus map and QTL projection

The maize IBM2 2008 Neighbors reference map was used as the consensus map in this study. BioMercator V4.2 (https://urgi.versailles.inra.fr/Tools/BioMercator-V4) was used to project original QTLs into the consensus map. The projection of QTLs was based on LOD scores, phenotypic variation explained by each QTL, confidence intervals and QTL positions. The positions of the 428 QTLs were obtained based on the genetic positions of flanking markers on the consensus map. Regarding markers without genetic positions, the closest markers of the QTL flanking markers from the reference were used to project QTL on the consensus map. The 95% confidence intervals (CI) of original QTLs on their original maps were estimated using the approach described by Darvasi and Soller (1997), i.e. CI = $530/NR^2$. Where N is the population size and R^2 is the proportion of the phenotypic variance explained by each QTL. Those QTLs which cannot be mapped onto the consensus map or the mapped location beyond the consensus map were discarded.

Meta-QTL analysis

Meta-analysis was performed according to the QTL clusters for each chromosome using BioMercator V4.2 (Goffinet and Gerber 2000; Sosnowski et al. 2012). The position and CI of each original QTL were projected on the consensus map using the homothetic function (Chardon et al. 2004). The Akaike Information Criterion (AIC) was used to select QTL models on each chromosome. According to the AIC value, the QTL model with the lowest AIC value was considered as a significant model. The position and 95% confidence intervals of each meta-QTL was calculated.

Identification of maize root candidate genes

Some cloned rice genes related to the root architecture were collected on the NCBI (https://www.ncbi.nlm.nih.gov/) and the protein sequences were downloaded from the Ricedata (http://www.ricedata.cn/gene/). *Arabidopsis* genes related to the root architecture were also collected on the NCBI (https://www.ncbi.nlm.nih.gov/) and iRootHair (www.iroothair.org), and the protein sequences were downloaded from the TAIR (https://www.arabidopsis.org/). The homologous sequences in maize were identified by using BLAST (https://blast.ncbi.nlm.nih.gov/Blast.cgi). Protein sequence alignment was conducted in BLAST by default e-value (e^{-10}), and homologous genes with rice and *Arabidopsis* root genes were identified with identity $> 40\%$ and coverage $> 60\%$ length alignment (Jiang et al. 2016). Sequences for candidate genes were collected from the MaizeGDB database (http://maizegdb.org/).

Results

Overview of collected QTLs

Reported QTLs for 23 root-related traits were surveyed from 20 independent studies (Table 1). These studies covered different experimental populations, and the population size ranged from 75 to 866 individual genotypes. The treatments included water stress (4 studies), nitrogen levels (3 studies), phosphorus levels (3 studies) and temperature stress (2 studies) and the others under normal growth conditions (Table 1). These populations were grown in three different media, including hydroponics (12 studies), natural soil (7 studies) and artificially mixed soil (3 studies) mainly in pots. The QTL information including flanking markers, phenotypic variation explained by each QTL and confidence intervals was

Table 1 List of references used for this study

Cross	Population type	Trait	Media	Stress treatment	QTL number	References
Lo964 × Lo1016	$F_{2:3}$	PRL PRW	Hydroponics on plastic tanks	Water	22	Tuberosa et al. (2002)
Lo964 × Lo1016	$F_{2:4}$	PRW	Hydroponics in PVC columns	Temperature	1	Hund et al. (2004)
B73 × Mo17	RIL	LRL LRN	Hydroponics in paper rolls	Phosphorus	12	Zhu et al. (2005)
B73 × Mo17	RIL	SRL SRN	Hydroponics in paper rolls	Phosphorus	32	Zhu et al. (2006)
Zong3 × 87-1	RIL	TRL RSA	Hydroponics		3	Ju et al. (2006)
HZ32 × K12	$F_{2:3}$	RDW TRL	Soil in pots	Water	17	Qiu et al. (2007)
B73 × *Zea luxurians*	F_2	RA	Soil in pots		10	Omori and Mano (2007)
Z3 × 87-1	RIL	LRL ARL ARN	Hydroponics in paper rolls	Nitrogen	7	Liu et al. (2008)
082 × Ye107	$F_{2:3}$	RDW	Soil in field	Phosphorus	7	Chen et al. (2008)
CML444 × CIMMYT	RIL	CRN PRL	Hydroponics in plastic containers	Water	9	Trachsel et al. (2009)
Ye478 × Wu312	BC_4F_3	RDW RSA TRL ARL ARN	Soil in field		28	Cai et al. (2012)
HZ32 × K12	$F_{2:3}$	TRL RDW	Soil in pots	Water	20	Osman et al. (2013)
B73 × Mo17 (IBM)Oh43 × W64a (OhW)	RIL	CRL SRN RDW PRL	Soil in pots		11	Burton et al. (2014)
Ny821 × H99 (NyH)						
Ye478 × Wu312	RIL	SRN CRN LRN PRL SRL CRL RDW	Hydroponics in plastic tub	Nitrogen	112	Li et al. (2015)
Ye478 × Wu312	BC_4F_3	TRL ARL LRL PRL ARN RDW	Hydroponics in paper roll	Nitrogen	28	Li et al. (2016b)
B73 × Mo17	RIL	PRL	Hydroponics in paper rolls	Temperature	6	Hu et al. (2016)
B73 × Gaspé	RIL	CRN PRW PRL SRN	Hydroponics in paper rolls		10	Salvi et al. (2016)
Zheng58 × Chang7-2	RIL	SRN SRL TRL CRL PRL SRL	Hydroponics in paper roll		10	Song et al. (2016)
Ye478 × Wu312	F_8	RDW PRL SRL SRN CRL CRN LRL	Paper roll, Hydroponics and Vermiculite		38	Liu et al. (2017)
Teosinte-W22	BC_2F_3	BRLN BRN BRNPL CRLN CRN CRNPL TCBRLN TCBRN TCBRNPL	Soil in field		134	Zhang et al. (2018)

Table 2 List of traits evaluated in the present study

Trait	Definition	No. of QTLs
PRL	Primary root length	45
PRW	Primary root weight	10
SRL	Seminal root length	34
SRN	Seminal roots number	54
BRN	Brace root number	19
BRLN	Brace root layers number	11
BRNPL	Brace roots number per layer	15
CRL	Crown root length	26
CRN	Crown roots number	41
CRLN	Crown root layers number	7
CRNPL	Crown roots number per layer	9
CRW	Crown root weight	7
LRL	Lateral root length	25
LRN	Lateral roots number	18
TCBRN	Total crown and brace root number	29
TCBRLN	Total crown and brace root layer number	20
TCBRNPL	Total crown and brace root number per layer	17
ARL	Axial root length	14
ARN	Axial roots number	9
RA	Root angle	10
RSA	Root surface area	7
TRL	Total roots length	36
RDW	Root dry weight	54

extracted from 517 QTLs for the 23 maize root traits from these published papers. When the original QTLs were projected into the target map, 89 QTLs could not be projected. Finally, 428 QTLs were used in the meta-analysis. These QTLs distributed randomly on the ten chromosomes, with the total number of QTLs per chromosome, ranging from 24 (Chr. 9) to 53 (Chr. 2). Chromsomes 1, 2 and 7 with relatively high number of QTLs (50, 53 and 50, respectively) affecting root traits, were shown affections on root traits (Fig. 1). The 428 QTLs were classified based on the percentage of the phenotypic variance explained by each QTL (Fig. 2). A total of 328 (76.6%) of the 428 QTLs displayed an R^2 value of less than 10%, while 100 QTLs (23.4%) explained more than 10% of the phenotypic variance (Fig. 2). Of these 428 QTLs, the number of QTLs for individual trait ranged from 3 for primary root weight to 45 for root dry weight and seminal root number.

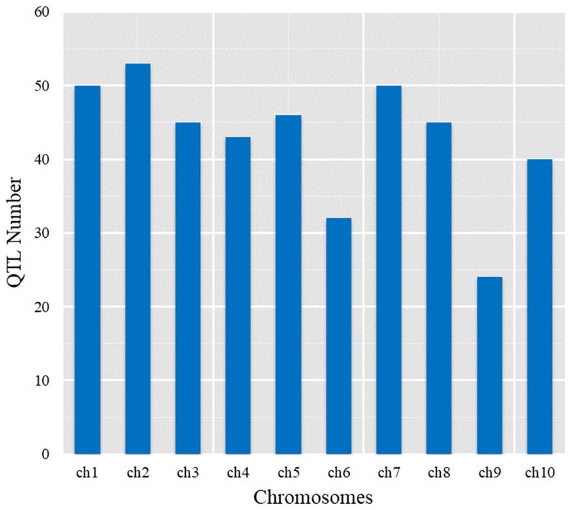

Fig. 1 The number of QTLs distributed on each chromosome

Meta-analysis

The collected root-related QTLs were projected into the consensus map by the BioMercator 4.2 software.

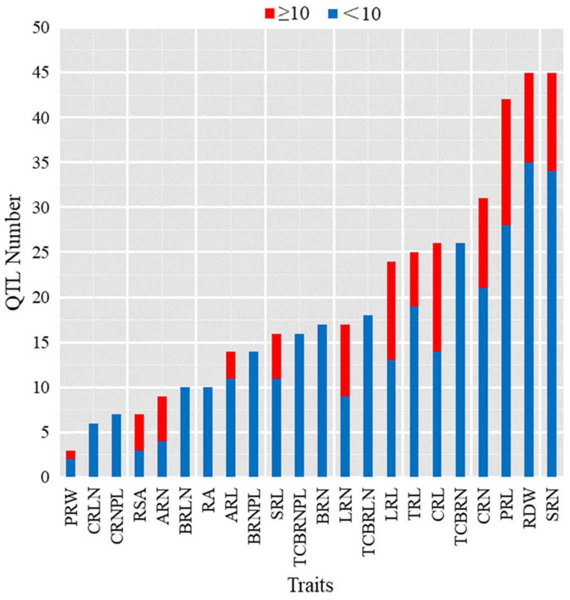

Fig. 2 The number of QTLs with different phenotypic variance explained (R2) for each trait collected in this study

Meta-analysis was conducted based the 428 QTLs for the 23 root-related traits, and a total of 53 MQTLs were identified according to the lowest Akaike Information Criterion (AIC) values criteria. Those MQTLs were unevenly distributed over all chromosomes. The number of MQTLs ranged from 2 on Chr. 7 and 9 to 10 on Chr. 5 (Fig. 3). There were three MQTLs on Chr. 1 and 4, 9 on Chr. 9, 6 on Chr. 2, 6, 8, and 10 (Table 3). The 95% CIs of all MQTLs ranged from 0.12 cM ($MQTL_{5-10}$) to 87.88 cM ($MQTL_{3-8}$), with an average of 16.59 cM. The physical intervals of the MQTLs varied from 45.7 kb to 28.4 Mb, and the interval of 32 MQTLs were less than 5 Mb. Those MQTLs with less than 5 Mb physical intervals were considered to be important regions for identifying candidate genes related to maize root traits. The number of the original QTLs per MQTL varied from two ($MQTL_{3-1}$, $MQTL_{6-2}$, $MQTL_{8-3}$ and $MQTL_{10-1}$) to twenty-two ($MQTL_{7-2}$), with the average of eight. More than 20 original QTLs were integrated on each of five MQTLs on bin 1.02 ($MQTL_{1-1}$), 4.03 ($MQTL_{4-1}$), 7.00 ($MQTL_{7-1}$), 7.04 ($MQTL_{7-2}$) and 9.02 ($MQTL_{9-1}$), respectively.

Mining of candidate genes in MQTLs

Compared with previously published genes associated with root-related traits in maize, only one reported gene, i.e. *rum1*, was located in $MQTL_{3-9}$ interval, whose mutant is defective in seminal root initiation and lateral root initiation on the primary root.

Functionally characterized genes related to root development were collected from rice and *Arabidopsis* to identify the homologous genes from the MQTL regions in maize. A list of maize homologs was collected corresponding to the genes affecting the root system architecture in rice and *Arabidopsis*. Through the investigation of the literature, in total 47 root-related genes cloned and functionally characterized were collected from the rice genome. A total of 47 maize homologs were identified from rice root-related genes (Supplementary Table S1). Five of the 47 rice genes, including *OsAUX1*, *SRT5*, *OsRAA1*, *OsCKX4* and *OsKTN80a*, had two homologous genes, thirty-eight genes have only one homologous gene in maize, four gene have no homologs. By integrating the physical positions of 47 maize homologs with 53 MQTLs, a total of four MQTLs regions were found to include nine maize homologs corresponding to seven rice genes (Table 4). Three candidate genes including GRMZM2G312738, GRMZM5G842970 and GRMZM5G877884 were located at the $MQTL_{1-3}$ region. The $MQTL_{3-8}$ region contained maize homologs GRMZM2G044055 and RMZM2G014653 corresponding to rice *OsFH1* and *OsNAC6*, respectively. One candidate gene GRMZM5G832135 was identified at the $MQTL_{5-10}$ region, which was homologous to *OsRHL1*. *SPR1* homolog (GRMZM5G813206) and *OsCKX4* homologs (GRMZM2G167220, GRMZM2G467069) were located at the $MQTL_{8-5}$ region (Supplementary Table S1). These mentioned rice genes have been shown to control root hairs and crown root development in previous studies. Therefore, these homologous genes might play important roles on maize root development or have similar function in maize.

Meanwhile, we collected 225 maize homologs corresponding to 271 *Arabidopsis* root-related genes through protein-protein BLAST method (Supplementary Table S2). In total, 36 maize homologs were obtained corresponding to 31 *Arabidopsis* root genes involving in lateral root, root hair growth and hormone regulation. In detail, these maize homologs were located at 17 MQTLs regions (Table 5). The thirty-eight maize homologous genes were annotated and categorized into 55 significant GO terms (Supplementary Fig. S1). The most significantly GO terms were enriched into root development (GO:0048364),

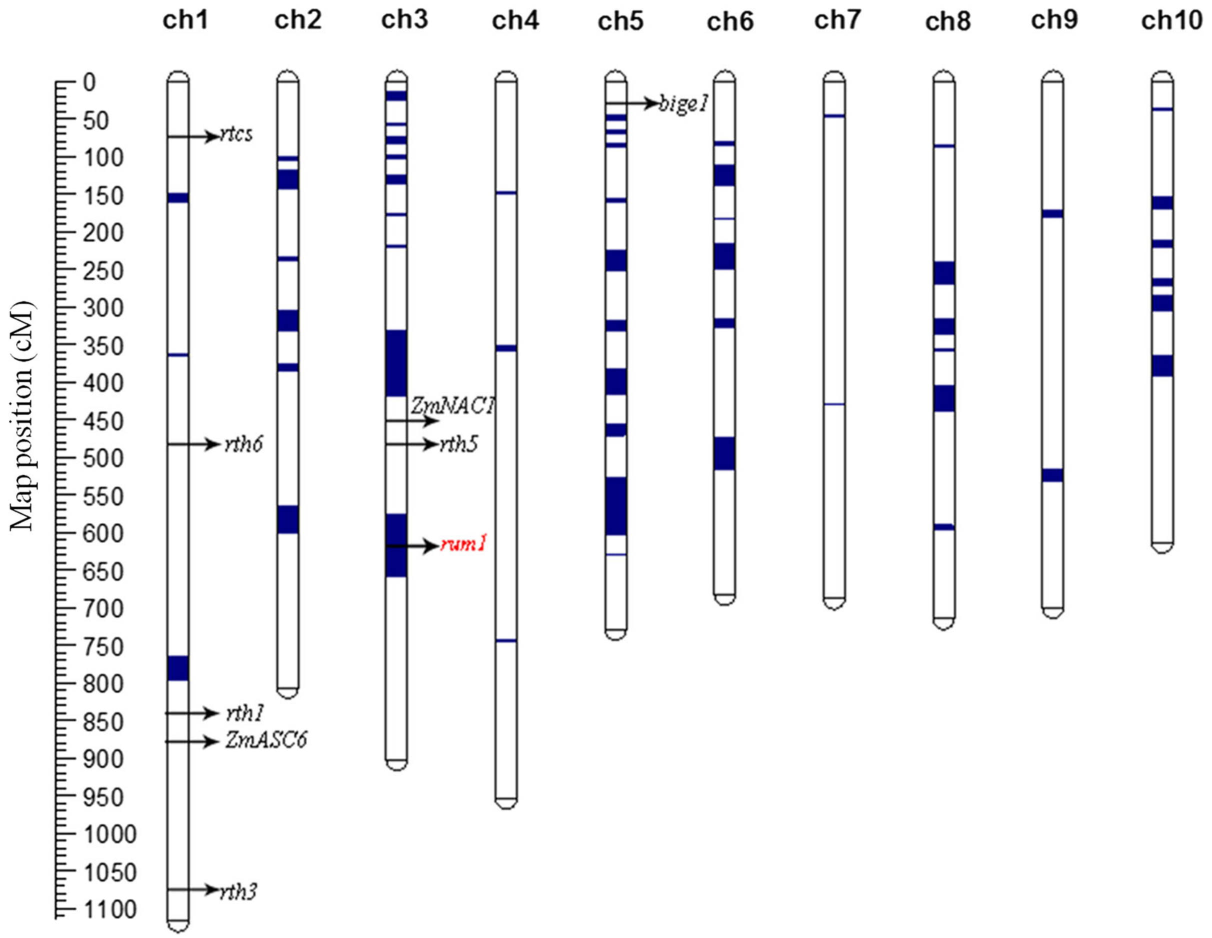

Fig. 3 The positions of the 53 MQTLs for root-related traits in this study. The 95% confidence intervals of these MQTLs is shaded in blue color. The red on the chromosome indicates maize root gene *rum1*, and the black indicates other genes influencing maize root development

epidermal cell differentiation (GO:0009913), and phosphorylation (GO:0016310).

Discussion

Meta-analysis is an effective approach to incorporate QTLs data from diverse studies and refine QTL confidence interval. In the previous study, 24 MQTLs were identified by compiling a total of 161 QTLs associated with maize root traits from 15 studies of nine mapping populations (Hund et al. 2011). In order to systematically identify genomic regions controlling root architecture in maize, we collected a total of 517 QTLs for root-related traits published over the past about 20 years, and 53 MQTLs were identified according to the lowest AIC values criteria. Our results showed that the confidence intervals of these MQTL have been greatly reduced. Compared with Hund's studies, seventeen of the 53 MQTLs overlapped with those reported by Hund et al. (2011) (Supplementary Table S3). These consistent QTL hotspots would be useful in MAS. Five of these overlapping MQTLs (MQTL$_{2\text{-}6}$, MQTL$_{3\text{-}8}$, MQTL$_{6\text{-}1}$, MQTL$_{10\text{-}3}$ and MQTL$_{10\text{-}6}$) have some QTLs mainly controlling the axial roots, which may be important regions for the fine-mapping of maize axial roots-related genes.

In this study, five of these identified MQTLs (MQTL$_{1\text{-}1}$, MQTL$_{4\text{-}1}$, MQTL$_{7\text{-}1}$, MQTL$_{7\text{-}2}$ and MQTL$_{9\text{-}1}$) contained a large number of the original QTLs. The MQTL$_{7\text{-}1}$, MQTL$_{7\text{-}2}$ and MQTL$_{9\text{-}1}$ with

Table 3 Results of meta-analysis of QTLs controlling root-related traits in maize

MQTL	Bin	Map position (cM)[a]	Physical distance (Mb)[b]	CI(95%)	No. of QTLs[c]	Trait involved
MQTL$_{1-1}$	bin1.02	149.1–160.16	17.46–21.57	5.53	22	PRL, BRLN, BRN, BRNPL, CRL, CRNPL, TCBRLN, TCBRN, TCBRNPL, TCBRN, TRL
MQTL$_{1-2}$	bin1.04	361.62–364.78	68.57–69.10	1.58	13	PRW, CRN, LRL, LRN, ARL, TRL, RDW
MQTL$_{1-3}$	bin1.08	765.33–795.39	235.63–246.41	15.03	15	CRL, CRN, RSA, SRL, SRN, LRL, ARL, TRL, RDW
MQTL$_{2-1}$	bin2.02	101.28–105.94	9.09–9.55	2.33	14	PRL, SRL, SRN, BRN, BRNPL, CRLN, CRN, CRNPL, TCBRLN, TCBRN, TCBRNPL
MQTL$_{2-2}$	bin2.02	117.89–142.95	10.48–12.11	12.53	10	PRL, SRL, BRLN, CRN, TCBRN, TCBRLN, RA, TRL, RDW
MQTL$_{2-3}$	bin2.03	234.48–237.68	26.63–27.51	1.6	4	PRL, SRN, CRN, RDW
MQTL$_{2-4}$	bin2.04	304.44–332.08	47.72–65.56	13.82	7	SRL, SRN, LRN, RA
MQTL$_{2-5}$	bin2.06	375.01–384.89	164.08–183.99	4.94	12	SRN, CRL, LRL, LRN, ARL, TRL, RDW
MQTL$_{2-6}$	bin2.09	564.64–599.66	218.01–225.23	17.51	6	PRL, SRL, SRN, LRL, ARL, TRL
MQTL$_{3-1}$	bin3.01	14.42–24.18	2.08–2.68	4.88	2	SRN, CRL
MQTL$_{3-2}$	bin3.01	56.81–57.37	3.84–3.89	0.28	5	PRL, BRLN, BRN, TCBRN, TCBRLN
MQTL$_{3-3}$	bin3.02	73.3–83.1	5.61–5.85	4.9	7	PRL, SRN, CRN, TCBRN
MQTL$_{3-4}$	bin3.02	98.21–102.45	7.60–8.21	2.12	5	PRL, BRN, BRLN, BRNPL, TCBRLN
MQTL$_{3-5}$	bin3.03	125.03–137.11	9.31–12.20	6.04	4	BRNPL, TCBRN, TCBRNPL, RDW
MQTL$_{3-6}$	bin3.04	176.25–179.53	20.47–21.86	1.64	6	PRL, SRL, CRL, ARN, RDW
MQTL$_{3-7}$	bin3.04	218.61–220.45	37.67–40.32	0.92	7	CRL, CRN, ARN, RDW
MQTL$_{3-8}$	bin3.05-3.06	330.6–418.48	148.43–176.85	43.94	5	PRL, LRL, ARL, TRL
MQTL$_{3-9}$	bin3.08	577.34–657.82	204.43–214.36	40.24	4	LRL, RDW
MQTL$_{4-1}$	bin4.03	147.78–150.24	13.41–17.53	1.23	23	PRL, SRL, BRN, BRNPL, CRL, CRN, CRNPL, LRL, LRN, TCBRN, TCBRLN, TCBRNPL, RDW
MQTL$_{4-2}$	bin4.06	352.09–359.35	154.65–155.86	3.63	12	PRL, SRL, SRN, CRL, RA,, TRL RDW
MQTL$_{4-3}$	bin4.11	743.57–743.91	240.89–241.17	0.17	8	PRL, SRN, CRN, LRL, RSA, TRL, RDW
MQTL$_{5-1}$	bin5.00	45.29–51.23	2.14–2.59	2.97	4	SRN, CRNPL, TCBRLN
MQTL$_{5-2}$	bin5.00-5.01	64.8–69.62	2.86–3.43	2.41	7	BRNPL, TCBRN, TCBRNPL, RSA
MQTL$_{5-3}$	bin5.01	82.9–88.28	4.20–4.59	2.69	3	SRN, CRL, CRLN
MQTL$_{5-4}$	bin5.01	155.3–161.52	9.41–10.18	3.11	6	SRL, SRN, TCBRN, TRL
MQTL$_{5-5}$	bin5.03	225.01–251.71	19.73–34.11	13.35	7	PRL, SRN, CRL, LRL, TRL
MQTL$_{5-6}$	bin5.04	319.2–332.5	135.34–155.57	6.65	4	PRL, SRN, CRL, RDW
MQTL$_{5-7}$	bin5.04-5.05	382.74–417.02	171.02–180.93	17.14	3	LRL, RDW
MQTL$_{5-8}$	bin5.05-5.06	454.85–471.77	188.15–192.30	8.46	6	CRL, CRN, ARL, RDW
MQTL$_{5-9}$	bin5.07	526.37–603.13	203.26–211.23	38.38	3	PRL, RDW
MQTL$_{5-10}$	bin5.08	629.92–630.04	212.42–213.87	0.06	3	PRL, SRN, RDW
MQTL$_{6-1}$	bin6.01	81.56–85.4	14.98–33.13	1.92	7	SRN, BRLN, TCBRN, TCBRLN, ARL, ARN
MQTL$_{6-2}$	bin6.01-6.02	112.46–139.58	71.11–89.29	13.56	2	PRL
MQTL$_{6-3}$	bin6.04	182.44–183.24	104.02–104.80	0.4	8	PRL, RSA, ARN, TRL, RDW

Table 3 continued

MQTL	Bin	Map position (cM)[a]	Physical distance (Mb)[b]	CI(95%)	No. of QTLs[c]	Trait involved
MQTL$_{6\text{-}4}$	bin6.04-6.05	216.61–249.81	109.71–124.33	16.6	2	CRN, RDW
MQTL$_{6\text{-}5}$	bin6.05	316.63–326.19	144.47–147.41	4.78	4	ARL, ARN, TRL, RDW
MQTL$_{6\text{-}6}$	bin6.07	473.7–515.74	162.80–165.09	21.02	9	PRL, SRN, CRL, LRL, LRN,
MQTL$_{7\text{-}1}$	bin7.00	45.03–47.13	3.03–3.19	1.05	23	PRL, BRN, BRLN, BRNPL, CRL, TCBRN, TCBRLN, TCBRNPL, LRN, RDW
MQTL$_{7\text{-}2}$	bin7.04	428.95–429.33	158.18–159.17	0.19	27	PRL, SRL, SRN, CRL, CRN, LRN, ARL, RA, RSA, TRL, RDW
MQTL$_{8\text{-}1}$	bin8.01	84.04–86.56	7.43–8.27	1.26	15	BRN, CRN, CRLN, CRNPL, TCBRN, TCBRLN, TCBRNPL
MQTL$_{8\text{-}2}$	bin8.03	241.47–269.11	79.74–100.38	13.82	9	PRL, SRN, CRL, CRN, LRN, RDW,
MQTL$_{8\text{-}3}$	bin8.05	315.22–335.94	115.14–122.48	10.36	2	PRL, LRL,
MQTL$_{8\text{-}4}$	bin8.05	356.86–357.16	129.49–130.27	0.15	3	PRW, SRN
MQTL$_{8\text{-}5}$	bin8.06	404.29–438.05	153.99–163.62	16.88	6	CRL, CRN, LRL, ARL, RDW
MQTL$_{8\text{-}6}$	bin8.08	589.76–595.5	172.67–172.96	2.87	10	SRL, CRL, CRN, LRL, LRN, ARL, TRL
MQTL$_{9\text{-}1}$	bin9.02	171.47–180.09	20.71–22.79	4.31	20	PRL, SRL, SRN, BRN, BRLN, CRN, CRLN, LRL, TCBRN, TCBRNPL, TRL, RDW
MQTL$_{9\text{-}2}$	bin9.06	516.61–532.47	141.23–148.48	7.93	4	SRL, LRN, TRL
MQTL$_{10\text{-}1}$	bin10.01	35.84–38.76	2.79–3.07	1.46	10	BRN, BRLN, BRNPL, CRN, CRLN, CRNPL, TCBRN, TCBRLN, TCBRNPL
MQTL$_{10\text{-}2}$	bin10.03	153.97–169.73	10.73–19.34	7.88	3	ARL, PRL
MQTL$_{10\text{-}3}$	bin10.03	211.4–220.08	78.33–83.47	4.34	9	PRL, SRL, SRN, LRL, ARL, RA, RDW
MQTL$_{10\text{-}4}$	bin10.04	261.89–271.39	112.60–114.72	4.75	5	PRL, CRL, RDW
MQTL$_{10\text{-}5}$	bin10.04	285.25–305.41	121.77–127.59	10.08	2	ARN, TRL
MQTL$_{10\text{-}6}$	bin10.06	364.12–392.04	136.08–139.15	13.96	11	PRL, SRN, CRL, ARN, RA, RSA, RDW

[a] The most probable position of the MQTL on the IBM2 2008 Neighbors map

[b] The confidence interval of the MQTL

[c] The number of the QTLs contained in the MQTL region

intervals less than 3 Mb and the original QTLs found in four to six mapping populations, may be hotspots affecting root-related traits, which is worth of intensive studies in the near future. Especially, MQTL$_{7\text{-}2}$ and MQTL$_{9\text{-}1}$ were involved in tolerance to nitrogen and phosphorus stress, including four original QTLs with CRL, CRN, LRL and ARL under nitrogen stress, and one original QTL with SRL under phosphorus stress. Zhu et al. (2006) reported that SRL was increased by 38% at low phosphorus. Moreover, Saengwilai et al. (2014) suggested that low CRN to enhance N acquisition from low-N soils. And, low-N stress could also increase LRL, PRL and ARL (Li et al. 2016b). Therefore, these genomic regions are very important when considering MAS for root-related traits breeding for more efficient nitrogen and phosphorus maize genotypes.

The ultimate aim of studying maize root system is to understand its role and potential in improving grain yield. Grain yield is more closely related to root system architecture (included TRL, ARL and ARN) at the early developmental stages of maize plants (Cai et al. 2012). Landi et al. (2002) also found a positive relationship between agronomic traits and roots. For

Table 4 Seven identified root-related genes in rice and their maize orthologs in MQTL regions

Gene name	Gene ID	Homologous gene ID in maize	MQTL	Bin Region	Reference
OsKTN80a	Os10g35200.1	GRMZM5G842970	$MQTL_{1\text{-}3}$	bin1.08	Wan et al. (2014)
		GRMZM5G877884	$MQTL_{1\text{-}3}$	bin1.08	
OsHOS1	Os03g52700.1	GRMZM2G312738	$MQTL_{1\text{-}3}$	bin1.08	Lourenco et al. (2016)
OsFH1	Os01g67240.1	GRMZM2G044055	$MQTL_{3\text{-}8}$	bin3.05-3.06	Huang et al. (2013)
OsNAC6	Os01g66120.1	GRMZM2G014653	$MQTL_{3\text{-}8}$	bin3.05-3.06	Lee et al. (2017)
OsRHL1	Os06g08500.1	GRMZM5G832135	$MQTL_{5\text{-}10}$	bin5.08	Ding et al. (2009)
SPR1	Os01g67290.1	GRMZM5G813206	$MQTL_{8\text{-}5}$	bin8.06	Jia et al. (2011)
OsCKX4	Os01g71310.1	GRMZM2G167220	$MQTL_{8\text{-}5}$	bin8.06	Gao et al. (2014)
		GRMZM2G467069	$MQTL_{8\text{-}5}$	bin8.06	

co-locations of QTLs between root and yield traits, one QTL *root-yield-1.06* was found by Landi et al. (2010), and was suggested to be a valuable candidate for MAS. In this study, 23 MQTLs for root architecture overlap 25 MQTLs for maize yield reported by Wang et al. (2016) (Supplementary Table S3), which suggested that these regions might have pleiotropic effects on the important agronomic traits, i.e. controlling both grain yield and root in maize. Six of these overlapping MQTL regions ($MQTL_{1\text{-}2}$, $MQTL_{2\text{-}5}$, $MQTL_{2\text{-}6}$, $MQTL_{3\text{-}8}$, $MQTL_{5\text{-}2}$, $MQTL_{10\text{-}6}$) have been reported in three different studies (Supplementary Table S3), suggesting that these regions could be used as important multi-effect QTL hotspots in the future studies.

Several genome-wide association studies (GWAS) have reported a number of single nucleotide polymorphism (SNPs) significantly associated with maize root traits (Pace et al. 2015; Zaidi et al. 2016; Sanchez et al. 2018). Pace et al. (2015) identified 263 SNPs associated with root traits at the seedling stage. Sanchez et al. (2018) found that 17 SNPs were indicated to be associated with maize root traits. In the present study, we compared the MQTL regions and those significantly associated SNPs (Supplementary Table S4). There were 14 SNPs located at 11 MQTLs regions, which were significantly associated with seedling root traits. Four of 14 SNPs associated with RDW were found in $MQTL_{2\text{-}2}$, $MQTL_{3\text{-}6}$, $MQTL_{6\text{-}5}$ and $MQTL_{8\text{-}5}$ regions.

To our knowledge, only a few maize root-related genes have previously been identified and cloned, due to the complexity of root growth and the difficulty of root phenotyping. Thus, we used the information of the cloned genes in rice (http://www.ricedata.cn/gene/) and *Arabidopsis* (https://www.arabidopsis.org/) to identify candidate genes and further understand the genetic basis of maize root-related traits. In the past several years, a number of rice root-related genes have been cloned, including *OsHOS1*, *OsKTN80a*, *OsFH1*, *OsNAC6*, *OsRHL1*, *SPR1*, *OsCKX4* and so on (Supplementary Table S1). In particular, *OsH0S1* regulates root curling (Lourenco et al. 2016) while *OsKTN80a* delays root growth of rice seedling by the repressed cell elongation in the elongation zone (Wan et al. 2014). *OsFH1* is required for the elongation of root-hairs in rice (Huang et al. 2013). The *OsNAC6* gene was reported to increased root number and root diameter (Lee et al. 2017). The *OsRHL1* gene controls root hair formation and development (Ding et al. 2009). Rice mutant *SPR1* has short postembryonic roots, including adventitious and lateral roots (Jia et al. 2011). *OsCKX4* gene affects crown root development by integrating the interaction between cytokinin and auxin (Gao et al. 2014). These rice root genes have been validated to have effect on root hairs, crown root, lateral root or root cell. Through the comparison between maize homologs and seven rice root genes, nine candidate genes for maize root-related traits were successfully predicted (Supplementary Table S1). Three candidate genes including GRMZM5G813206 (homolog to *SPR1*), GRMZM2G167220 and GRMZM2G467069 (homologs to *OsCKX4*) located in the $MQTL_{8\text{-}5}$ region, seem to be suitable for future studies on maize lateral root and crown root. Meanwhile, to identify maize root candidate genes, a

Table 5 Thirty-one identified root-related genes in *Arabidopsis* and their maize orthologs in MQTL regions

Gene name	Gene ID	Homologous gene ID in maize	MQTL	Bin Region	Reference
VLN4	AT4G30160	GRMZM2G053839	MQTL$_{2-2}$	bin2.02	Du et al. (2011)
TIR1	AT3G62980	GRMZM5G848945	MQTL$_{2-4}$	bin2.04	Perez-Torres et al. (2008)
ANP2	AT1G54960	GRMZM2G098828	MQTL$_{2-5}$	bin2.06	Beck et al. (2010)
RHD2	AT5G51060	GRMZM2G065144	MQTL$_{2-6}$	bin2.09	Takeda et al. (2008)
		GRMZM2G037993			
		GRMZM2G358619			
WRKY75	AT5G13080	GRMZM2G106560			Rishmawi et al. (2014)
HKL1	AT1G50460	GRMZM2G068913	MQTL$_{3-8}$	bin3.05-3.06	Karve et al. (2012)
		GRMZM2G467069	MQTL$_{8-5}$	bin8.06	
AKT1	AT2G26650	GRMZM2G022915	MQTL$_{3-9}$	bin3.08	Li et al. (2017)
MRH1	AT4G18640	GRMZM2G078926			Jones et al. (2006)
PGP4/AtABCB4	AT2G47000	AC233882.1_FG003			Kubes et al. (2012)
PI4KBETA1	AT5G64070	GRMZM2G176698	MQTL$_{4-1}$	bin4.03	Sasek et al. (2014)
AXR1	AT1G05180	GRMZM2G002765	MQTL$_{5-1}$	bin5.00	Zhang and Forde (1998)
TUA6	AT4G14960	GRMZM2G152466	MQTL$_{5-4}$	bin5.01	Ishida and Hashimoto (2007)
CAP1	AT4G34490	GRMZM2G096596			Deeks et al. (2007)
PHYA	AT1G09570	GRMZM2G181028			Correll and Kiss (2005)
MRH5/SHV3/ GDPDL3	AT4G26690	GRMZM2G013324	MQTL$_{5-7}$	bin5.04-5.05	Hayashi et al. (2008)
		GRMZM2G021482			
		GRMZM2G038934			
AtHDG11	AT1G73360	GRMZM2G145690	MQTL$_{5-9}$	bin5.07	Xu et al. (2014)
AtPIN3	AT1G70940	GRMZM2G074267			Benkova et al. (2003)
PIN1	AT1G73590	GRMZM2G074267			Bao et al. (2004)
BST1	AT5G65090	GRMZM2G335930			Parker et al. (2000)
FEZ	AT1G26870	GRMZM2G100593			Willemsen et al. (2008)
		GRMZM2G401609			
TUP5	AT1G80600	GRMZM2G119583	MQTL$_{6-1}$	bin6.01	Fremont et al. (2013)
CRFs	AT2G46310	GRMZM2G328197	MQTL$_{6-2}$	bin6.01-6.02	To and Kieber (2008)
RHL1	AT1G48380	GRMZM2G406101			Schneider et al. (1998)
RHS10	AT1G70460	GRMZM2G442215	MQTL$_{6-4}$	bin6.04-6.05	Hwang et al. (2016)
AtHK3	AT1G27320	GRMZM2G423456			Werner et al. (2003)
MYA2	AT5G43900	GRMZM2G058155			Peremyslov et al. (2008)
BRN2	AT1G03457	GRMZM2G005459			Bennett et al. (2010)
RALF1	AT1G02900	GRMZM2G395429			Bergonci et al. (2014)
AtMPK4	AT4G01370	GRMZM2G123886	MQTL$_{10-3}$	bin10.03	Kosetsu et al. (2010)
OXI1	AT3G25250	GRMZM5G802115	MQTL$_{10-5}$	bin10.04	Rentel et al. (2004)
PGP19	AT3G28860	GRMZM2G125424	MQTL$_{10-5}$	bin10.04	Titapiwatanakun et al. (2009)

comprehensive list of maize homologous genes to *Arabidopsis* was also collected (Supplementary Table S2). In previous studies, it has been found that these *Arabidopsis* genes regulated hormones and cell differentiation involving in root development. Functional GO term annotations of the 36 maize homologs corresponding to the *Arabidopsis* root-related genes were related to root development, epidermal cell differentiation, and phosphorylation (Fig. S1). These results indicated that the root of maize and

Arabidopsis displayed similarities in the root development. Therefore, these maize homologous genes to rice and *Arabidopsis* genes could help to understand which regulatory processes and underlying genetic components would regulate root growth in maize. And these homologous genes would lay the foundation for elucidating the genetic control of the maize root system architecture.

Acknowledgements This research was supported by the Programs of MOST and MOA of China (2016YFD0101201, 2016YFD0100103, 2016YFD0100303, 2014BAD01B02), National Natural Science Foundation (91335206), Young Elite Scientists Sponsorship Program by CAST (2016QNRC001), and the CAAS Innovation Program.

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